Bird functional diversity in the Yangambi Biosphere Reserve, DR Congo

Stijn Cooleman[a,c], Frank Bapeamoni[b], Michel Louette[a], Luc Lens[c] and Upoki Angenong'a[b]

Diversité fonctionnelle des oiseaux dans la Réserve de Biosphère de Yangambi, RD Congo. Un inventaire des oiseaux du sous-bois a été fait dans la Réserve de biosphère de Yangambi, RD Congo, en septembre 2012, à l'aide de filets japonais. L'objectif était de comparer la présence des oiseaux en forêt primaire, en forêt secondaire et en forêt de transition dans cette zone tropicale humide de basse altitude. Au total, 51 espèces ont été capturées, dont la majorité étaient des spécialistes des forêts, y compris deux taxons quasi-endémiques au Bassin du Congo. L'abondance relative était légèrement plus élevée en forêt primaire qu'en forêt secondaire, et nettement plus faible dans la zone de transition. De 44 espèces forestières, 14 ont été trouvées uniquement en forêt primaire, dont 11 insectivores. L'abondance relative des insectivores diminue avec la dégradation de la forêt.

Summary. A survey of understorey bird species occurring in old-growth forest, regrowth forest and transition zones in the Yangambi Man and Biosphere Reserve, DR Congo, was carried out on 5–24 September 2012 using mist-nets. In total, 51 species were captured, the majority forest specialists, including two Congo Basin near-endemics. Relative abundance was slightly higher in old-growth forest than in regrowth forest, and distinctly lower in the transition zone. Of the 44 forest-dependent species, 14 were recorded only in old-growth forest, 11 of which were insectivores. Relative abundance of insectivores declined with forest degradation.

The tropical rainforest of the Congo Basin is a biodiversity hotspot, with >1,000 bird species recorded. Habitat degradation can have a severe impact on species presence, e.g. by causing changes in vegetation structure or shifts in food abundance. Such alterations are expected to affect different functional bird groups in different ways, with insectivores expected to be most sensitive to forest disturbance. In the Afrotropical region, this has been demonstrated for large insectivores (Fjeldså 1999), terrestrial or understorey insectivores (Sekercioğlu 2002, Waltert *et al.* 2005, Newmark 2006, Dunham 2008), ground-foragers (Dranzoa 1998, Dale *et al.* 1999), ant-followers (Waltert *et al.* 2005), leaf-gleaners (Owiunji & Plumptre 1998, Dale *et al.* 1999,Waltert *et al.* 2005), bark-gleaners (Dale *et al.* 1999) and some sallying insectivores (Plumptre 1997, Owiunji & Plumptre 1998). However, some studies suggest that certain insect predators increase with forest degradation, such as sallying insectivores at the forest edge (Dale *et al.* 1999), insect gleaners in moderately disturbed forest (Newmark 2006) and bark-gleaners in logged forest (Owiunji & Plumptre 1998). In one study, insectivores increased following logging in a regrowth forest (Owiunji 2001).

Few data are available on the effects of forest modification on the avian functional diversity and feeding guilds in the Congo Basin: just one study, undertaken in the Ituri Forest of north-eastern DR Congo (Plumptre 1997), is known to us. The effects have been more comprehensively documented elsewhere, e.g. in Cameroon (Waltert *et al.* 2005), Côte d'Ivoire (Dunham 2008), Tanzania (Fjeldså 1999, Newmark 2006) and Uganda (Dranzoa 1998, Owiunji & Plumptre 1998, Dale *et al.* 1999, Owiunji 2001, Sekercioğlu 2002, Naidoo 2004).

Study area

Yangambi Man and Biosphere Reserve (Y-MAB) is located on the Congo River, west of Kisangani (Tshopo District, Oriental Province), at *c.*500 m altitude. Covering *c.*235,000 ha, it is the largest of the three UNESCO Biosphere Reserves in DR Congo (*cf.* www.unesco.org/mabdb/bios1-2.htm). The reserve lies within the Guinea-Congo Forests biome, in the south-western part of the North-eastern Congolian Lowland Forests (Fishpool & Evans 2001, WWF 2012).

Y-MAB is the study area for the 'Congo Basin integrated monitoring for forest carbon mitigation and biodiversity' (COBIMFO) project, which aims to establish possible links between

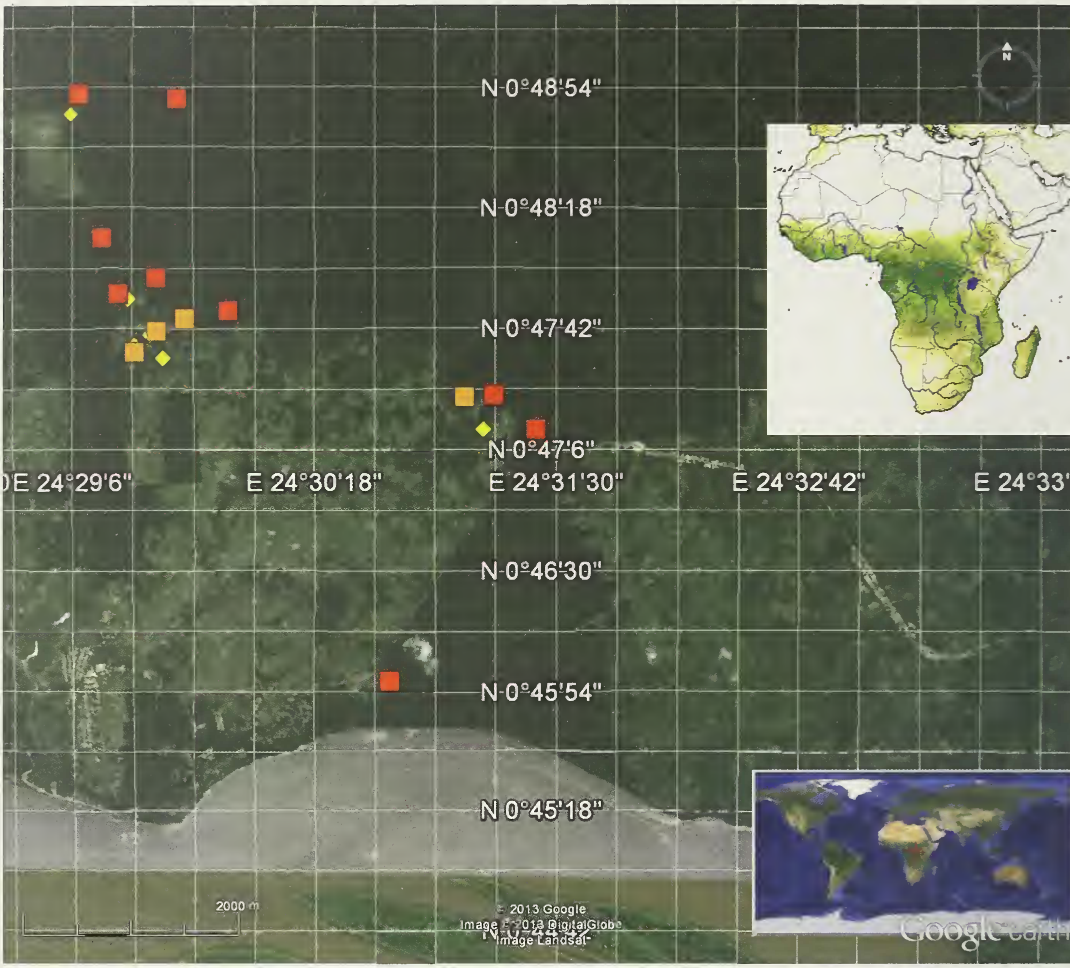

Figure 1. Location of the study area in the Yangambi Biosphere Reserve (red point on inset map; © RCMA), DR Congo, with the 19 survey sites (red square = old-growth forest, orange square = regrowth forest, yellow diamond = transition zone); © Google Image 2013, © DigitalGlobe Image Landsat 2013.

Localisation de la zone d'étude comprenant 19 sites d'inventaire, catégorisés en trois principaux types d'habitat (symboles : carré rouge = forêt primaire, carré orange = forêt secondaire, losange jaune = zone de transition) dans la Réserve de Biosphère à Yangambi (point rouge sur l'encart ; © RMCA), RD Congo ; © Google Image 2013, © DigitalGlobe Image Landsat 2013.

carbon balance and biodiversity in pristine and deteriorated tropical rainforests. A recent report (Toirambe *et al.* 2010) includes a very incomplete bird species list. Our aim was to assess current avifaunal richness and investigate possible differences between habitat types, focusing on the presence and relative abundance of particular functional species groups, such as different forest-dependence classes and feeding guilds. This is not only potentially useful for improving bird conservation, but also permits predictions of changes in birds' ecosystem services (see Wenny *et al.* 2011 *in* Sekercioğlu 2012). Benefits to humans from ecosystems include invertebrate pest control by insectivores, pollination by nectarivores and seed dispersal by frugivores. Some economic activities occur within the reserve, causing human pressure (Toirambe *et al.* 2010) due to hunting, land-use changes and small-scale deforestation.

Due to difficulty of access to most areas, and political instability, data on the Congolese avifauna in general and that of the Yangambi region in particular are scarce (Demey & Louette 2001). The Royal Museum for Central Africa (RMCA) holds specimens from Yangambi and neighbouring localities, collected between the late 19th and mid-20th centuries (Schouteden 1948–60). However, the biological information accompanying these specimens is limited. During their ornithological exploration of the Congo River *c.*100 years ago, Chapin and Lang passed Yangambi, and investigated the area north-east of Kisangani (Chapin 1932). More recently, international collaboration has enabled some avian studies in the region, including random mist-netting during the Congo River Expedition of 2010 (Louette *et al.* 1995, Upoki 2001, Voelker *et al.* 2013, Bapeamoni 2014).

Here we report the findings of a mist-netting survey undertaken just north-east of the centre of Yangambi, at 00°45'–00°50'N 24°29'–24°32'E, on 5–24 September 2012, by the first two authors (Fig. 1). Nineteen sites within a c.2.5 km radius were selected: 13 forest sites and six sites in the transition zone. Main habitat types were:

- Old-growth forest (OGF; nine sites): mature forest (i.e. primary forest), with closed canopy, including subtypes differentiated by diagnostic species: one of *Gilbertiodendron* (climax forest with *G. dewevrei* dominant, typically with a sparse understorey), one of *Brachystegia* (climax forest with *B. laurentii* dominant, and a moderately open undergrowth) and seven of *Scorodophloeus* forest (comprising three 'mixed' and four 'edge' sites, in places with a very dense undergrowth).
- Regrowth forest (RGF; four sites in *Musanga* forest): young forest re-growing following disturbance (i.e. secondary forest), in places with an open canopy, including different stages of fragmentation and development (from fallow to young tall forest), consequently involving a greater habitat heterogeneity, adjacent to agricultural land at forest edges.
- Transition zone (TZ; six sites): mixed-rural habitat between forest and (post-)agricultural land, including thickets or very degraded forest patches.

These forest habitat types differ in vegetation structure, including canopy cover, and can be ordered along a successional vegetation gradient (basically from TZ via RGF to OGF). Abiotic and biotic parameters were sampled by members of the COBIMFO project via a plot-based design of various types.

Weather was relatively stable during the study period, the dry season lasting longer than usual, until the second half of September (rather than the end of August). The wet season commenced with some overnight showers and a few heavy downpours on several afternoons but, overall, the effects on field work were negligible.

Methods

Mist-netting

Twenty ground-level mist-nets were erected, spread over max. 3 adjacent sites simultaneously: 4–6 nets (i.e. 40–67 m) per RGF or OGF site, and 1–4 nets (i.e. 9–44 m) per TZ. Thus, max. 217 m of net length was in use simultaneously. Geographic coordinates of all mist-nets were recorded using a GPS. Opened nets were checked regularly during the daytime (between dawn, at *c.*06.00 hrs, and dusk, at *c.*18.00 hrs). Following 2–5 days at each site, nets were moved. Mist-nets were set for a total of 38,310 metre-net-hours (mnh), divided unevenly between the three main habitat types: 23,157 mnh in OGF, 9,425 mnh in RGF and 5,728 mnh in TZ. By taking the trap intensity in mnh into account, we calculated relative abundance as capture rate in numbers of birds per 100 mnh, to compare abundance between habitat types. Additional diversity indices were derived, such as species richness, as the absolute number of captured bird species, and Shannon-Wiener index, as a measure of species diversity taking into account the relative abundance of species present in the community, for each habitat type.

Trapped birds were mainly identified using Sinclair & Ryan (2010); difficult individuals were photographed, for subsequent identification using *The Birds of Africa* (*BoA*) handbooks (Brown *et al.* 1982, Urban *et al.* 1986, Fry *et al.* 1988, Urban *et al.* 1997, Fry *et al.* 2000, Fry & Keith 2004) and by examining specimens in the RMCA collection. Species mentioned between parentheses in Appendix 1 are still questionable and *Terpsiphone* (*viridis*) might include some individuals of Bates's Paradise Flycatcher *T. batesi*.

Bird groups

Bird species were assigned to functional groups based on habitat and food preferences (Appendix 1). Three classes of forest-dependence were used (according to Bennun *et al.* 1996, if listed, and additionally *BoA*) and six major feeding guilds, following principally Waltert *et al.* (2005) except two adjustments (for Speckled Tinkerbird *Pogoniulus scolopaceus* and Vieillot's Black Weaver *Ploceus nigerrimus*, due to their mixed food preferences) and based on *BoA*.

Results

Capture rates and diversity indices

In total, 576 individuals of 51 species were mist-netted (Appendix 1), with an overall capture rate of 1.504 birds/100 mnh. Capture rate was highest in OGF (1.589 birds/100 mnh), slightly lower in RGF (1.475 birds/100 mnh) and distinctly lower in TZ (1.205 birds/100 mnh). Between OGF subtypes, differences in relative abundance were subtle: slightly higher in *Gilbertiodendron* forest (1.758 birds/100 mnh) than in *Brachystegia* forest (1.722 birds/100 mnh), but rather lower in *Scorodophloeus* forest (1.537 birds/100 mnh).

Species richness was highest in OGF (minimum 32 species or *c*.61% of all captured species), lower in RGF (minimum 28 species or *c*.55% of all captured species) and lowest in TZ (minimum 17 species or *c*.33% of all captured species). Shannon-Wiener indices for both forest habitat types were higher than for TZ and slightly higher for RGF than for OGF.

Bird community composition

Pycnonotidae (bulbuls) was the dominant family (*c*.60% of all captures, with nine species), in every habitat type. Their aggregate capture rate increased from degraded habitat to mature forest. Yellow-whiskered Greenbul *Andropadus latirostris* (Fig. 2a), a widespread omnivorous bulbul, was the most abundant species (*c*.36%) in every habitat type.

Of the 51 mist-netted species, 35 are restricted to the Guinea-Congo Forests biome. Their relative abundances increased with forest age, with the largest proportion in OGF. This group included two near-endemics, Jameson's Antpecker *Parmoptila jamesoni* (Fig. 2g) and Grant's Bluebill *Spermophaga poliogenys* (Fig. 2h).

Forest-dependence

Forty-four species were forest-dependent: forest specialists (30) were slightly more abundant than forest generalists (14). The rest was formed by seven forest visitors or open-habitat species.

The relative abundance of forest specialists declined with forest degradation, whereas forest generalists were more abundant in degraded habitat. Capture rates of forest visitors or open-habitat species increased slightly with forest alteration.

The three habitats were dominated by forest-dependent classes. Within OGF, the majority was formed by forest specialists (0.941 birds/100 mnh), beside a notable proportion of forest generalists (0.613 birds/100 mnh) and just a few forest visitors (0.030 birds/100 mnh). RGF was intermediate, characterised by balanced proportions of the different classes of forest-dependence, of which forest generalists were most prevalent (0.891 birds/100 mnh). TZ supported a mixed avifauna of mainly generalists (0.855 birds/100 mnh). TZ's minority comprised remarkably more forest specialists (0.279 birds/100 mnh) than forest visitors or open-habitat species (0.087 birds/100 mnh).

Of the 44 forest-dependent species, 14 were captured only in OGF, of which 11, i.e. the majority, were insectivores. These insect predators consisted mainly of forest specialists: ten species, including African Dwarf Kingfisher *Ceyx lecontei*, African Piculet *Sasia africana* (Fig. 2d), Rufous-sided Broadbill *Smithornis rufolateralis* (Fig. 2e), Red-tailed Bristlebill *Bleda syndactylus* (Fig. 2c), Grey-headed Sunbird *Deleornis axillaris* (Fig. 2f) and Jameson's Antpecker, and one generalist (African Emerald Cuckoo *Chrysococcyx cupreus*). Additionally, just one insectivorous forest visitor (African Pygmy Kingfisher *Ceyx pictus*) was captured only in OGF. Thus, 12 insectivores were not trapped in degraded habitat. About half of the remaining insectivores, such as Icterine *Phyllastrephus icterinus* and Xavier's Greenbuls *P. xavieri* (Fig. 2b), occurred in smaller numbers in degraded habitat than in OGF. We trapped substantially fewer species and individuals of insectivores in degraded habitat.

Feeding guilds

Among feeding guilds (Fig. 3), insectivores had the highest species richness. The omnivores

Figure 2. Forest-dependent species in Yangambi Biosphere Reserve, DR Congo, September 2012: (**a**) Yellow-whiskered Greenbul / Bulbul à moustaches jaunes *Andropadus latirostris*; (**b**) Icterine Greenbul / Bulbul ictérin *Phyllastrephus icterinus* (in foreground) and Xavier's Greenbul / Bulbul de Xavier *Phyllastrephus xavieri*; (**c**) Juvenile Red-tailed Bristlebill / Bulbul moustac *Bleda syndactylus*; (**d**) Male African Piculet / Picumne de Verreaux *Sasia africana*; (**e**) Male Rufous-sided Broadbill / Eurylaime à flancs roux *Smithornis rufolateralis*; (**f**) Male Grey-headed Sunbird / Souimanga à tête grise *Deleornis axillaris*; (**g**) Female Jameson's Antpecker / Parmoptile de Jameson *Parmoptila jamesoni*; (**h**) Male Grant's Bluebill / Sénégali à bec bleu *Spermophaga poliogenys* (Stijn Cooleman)

comprised a similar but slightly lower proportion of relative abundance, with only five species (especially Yellow-whiskered Greenbul, the most frequently captured species). All four nectarivores were sunbirds (Nectariniidae), which have a mixed diet of nectar, fruits or berries and insects. The three major avian feeding guilds—i.e. insectivores, omnivores and nectarivores—were represented in all habitat types, potentially providing important ecosystem services.

Of the remaining species, only granivores (with six species, including Columbidae and the majority of the waxbills Estrildidae) were represented in all habitat types. The carnivores (two *Accipiter* species) and the only obligate frugivore (Yellow-rumped Tinkerbird *Pogoniulus bilineatus*) were captured only in forest sites and TZ, respectively.

Variations in feeding guilds' capture rates appear between the main habitats (Fig. 3). The relative abundance of insectivores declined markedly with forest degradation: it was much higher in OGF (0.777 birds/100 mnh or nearly half of all captures within OGF) than in RGF (0.594 birds/100 mnh or *c.*40% of all captures within RGF) or TZ (0.227 birds/100 mnh or *c.*19% of all captures within TZ). Capture rates of the four partially insectivorous Nectariniidae also declined, although less markedly, whilst those of the omnivores and granivores increased.

Discussion

Our study indicates that abundances of several dominant groups are affected by forest modification and land use, especially for bulbuls, biome-restricted species, forest specialists and insectivores. In line with most avian functional diversity studies in tropical forests (*cf.* Sekercioğlu 2012), insectivores comprise the majority in old-growth forest and less frequently in degraded or fragmented habitat. Forest generalists and omnivores showed opposite patterns and were more abundant in disturbed forest habitat. Such shifts involved substitutions within different functional groups and consequently similar total capture rates in old-growth and regrowth forest. Yet, the total capture rate per habitat appeared to decrease slightly with forest disturbance, as did the diversity indices (except the Shannon-Wiener index, which was marginally higher in regrowth forest).

Disturbance-sensitive groups were also dominant overall. Irrespective of habitat, insectivores comprised the greatest number of species among feeding guilds, whilst omnivores were represented by distinctly fewer species. However, overall abundances of insectivores and omnivores were similar. Thus, if guild species numbers alter, their relative abundances do not necessarily change equally (*cf.* Sekercioğlu 2012). With respect to forest-dependence classes, forest specialists had a markedly higher species richness and a slightly higher capture rate than generalists.

Comparisons among tropical forest avifaunas

Overall capture rate at Y-MAB was lower than in Ituri Forest (Plumptre 1997), Kibale National Park (Dranzoa 1998) and Budongo Forest Reserve (Ngabo & Dranzoa 2001, Owiunji 2001). In some of these forests, the capture rate of forest specialists was considerably higher than that of generalists (Dranzoa 1998, Ngabo & Dranzoa 2001). In contrast, Farwig *et al.* (2008) registered a higher proportion of generalist captures, but a higher species richness of forest specialists in Kenya's Kakamega Forest. As in other Afrotropical studies (*cf.* Waltert *et al.* 2005), the most dominant family was the Pycnonotidae. Their high capture rates may in part be explained by the social structure of the abundant Yellow-whiskered Greenbul possibly behaving as a lek species (Brosset 1982, 1990), their varied diet (Bapeamoni 2014) and their ability to occupy various ecological niches (Keith *et al.* 1992, Upoki 2001).

Biome-restricted species comprised the majority of captured species and were negatively correlated with the gradient of land-use intensity, as in Cameroon (Waltert *et al.* 2005).

Generally, our greater total capture rate in intact forest matches findings in Uganda (Ngabo & Dranzoa 2001), in contrast to the slightly higher capture success in secondary versus primary forest in Ituri (Plumptre 1997). Clearly contrary results were recovered by Dranzoa (1998) and Catry *et al.* (1999), who mist-netted an obviously higher proportion of avifauna in secondary forest (where more birds fly at net height) than in primary forest. As understorey birds are more readily captured in mist-nets (Woog *et al.* 2010), we estimate that their relative abundance declines with forest degradation, being highest in mature forest.

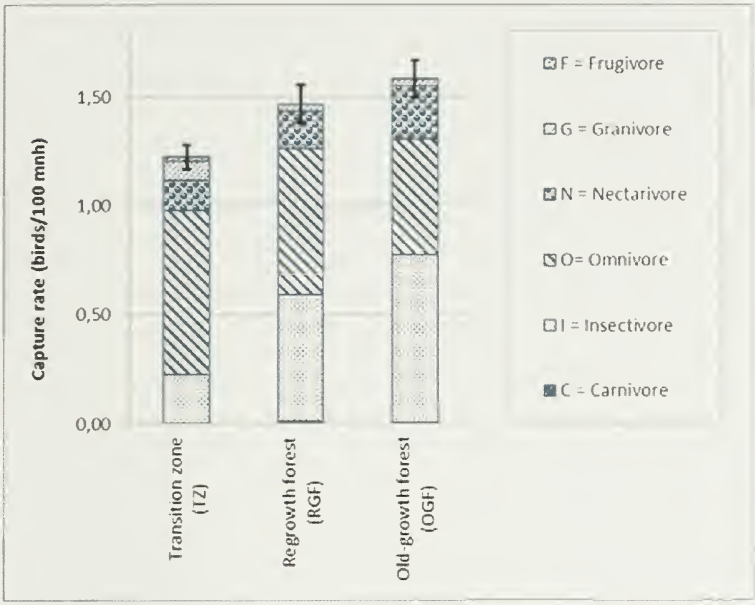

Figure 3. Relative abundance as capture rate (number of birds per 100 metre-net-hour) per feeding guild in each habitat. Error flags are applicable on the whole length of the plotted bars (calculated as mean values of the Shannon-Wiener indices of the sites within each main habitat type).

L'abondance relative exprimée par le taux de capture (nombre d'oiseaux par 100 mètre-filet-heure) par type de régime alimentaire et par type d'habitat. Des drapeaux d'erreur sont applicables sur toute la longueur des barres tracées (calculés comme des valeurs moyennes des indices de Shannon-Wiener des sites dans chaque principal type d'habitat).

Between old-growth forest subtypes, their relative abundance seems to decline with undergrowth density, but other vegetation structure parameters or distance to forest edge might influence this trend too.

Several studies have found that birds follow the expected gradient, with the most and least species-rich assemblages occurring in mature forests and degraded forest habitats, respectively (e.g. Thiollay 1995 *in* Waltert *et al.* 2005, Plumptre 1997, Lawton *et al.* 1998 *in* Waltert *et al.* 2005, Farwig *et al.* 2008), while others have uncovered opposite patterns (Dranzoa 1998, Catry *et al.* 1999, Fjeldså 1999, Dranzoa 2001, Sekercioğlu 2002). Yet, our species richness results must be interpreted with caution, due to the uneven capture intensity between the different main habitats: 28 species captured in regrowth forest in fewer than 10,000 mnh compared to 32 species in old-growth forest in more than 20,000 mnh. Although the species-time-area relationship almost always decreases, the species richness in regrowth forest should be higher in cases of similar capture rates.

Our diversity indices are probably somewhat biased by circumstances, notably the fact that some species were captured only once or twice, such as the forest specialist Yellow-browed Camaroptera *Camaroptera superciliaris* in degraded habitat alone. Some supposedly common generalists, such as Little Greenbul *Andropadus virens*, were rarely captured (possibly due to their relatively low capture rates in degraded habitats). Moreover, the Shannon-Wiener index demonstrated that both forest habitat types supported more avian diversity than the transition zone. The slightly higher Shannon-Wiener index for regrowth forest than for old-growth forest might reflect the greater habitat heterogeneity between regrowth forest sites (comprising fallow and young regrowth forest) than between old-growth forest sites. This comparison on a local scale within habitat clusters has also been considered by other studies (including Dranzoa 1998, Ngabo & Dranzoa 2001), proving that disturbance, including treefall gaps in vegetation, generates greater habitat heterogeneity. The combination of closed, reduced and open canopy, and increased open habitat in regrowth forest, permits a high abundance of forest visitors and generalists to occur, together with some forest specialists, as found by other studies (e.g. Sekercioğlu 2002).

Differences in relative abundance and diversity indices between both forest habitat clusters appear largely due to the substitution of some typical forest specialists (e.g. African Dwarf Kingfisher, Rufous-sided Broadbill and Jameson's Antpecker) in old-growth forest by more generalist species (such as Tambourine Dove *Turtur tympanistria*, Speckled Tinkerbird

Pogoniulus scolopaceus, Fraser's Forest Flycatcher *Fraseria ocreata* and Olive-bellied Sunbird *Cinnyris chloropygius*) or open-habitat species (e.g. Blue-spotted Wood Dove *Turtur afer* and Tawny-flanked Prinia *Prinia subflava*) in regrowth forest (*cf.* Lawton *et al.* 1998 *in* Waltert *et al.* 2005).

Different responses of bird groups

We found, like Sekercioğlu (2002), that forest specialists decline and generalists increase with forest degradation. Moreover, forest specialists were less abundant than generalists only in degraded habitat (including regrowth forest), as was true in a Kenyan study (Farwig *et al.* 2008). In contrast, forest specialists were (slightly) more abundant than generalists in logged or regenerating forests in Uganda (Dranzoa 1998, Naidoo 2004). These differences could be due to differences in methodology, or because the logged study area in Uganda was surrounded by more intact forest than most regrowth sites in Y-MAB. Furthermore, some unexpected captures were made in the transition zone, e.g. Xavier's Greenbul, a forest specialist. This mobile species moves freely from forest into open, degraded, logged or mixed-rural habitats, as evidenced elsewhere for many forest birds in general (Dranzoa 1995 *in* Sekercioğlu 2002, Naidoo 2004) and some old-growth sites in our study area were situated on the forest edge. On the other hand, several generalist and even a few open-habitat species were captured in old-growth forest (especially in *Gilbertiodendron* forest with a relatively sparse understorey).

Although our survey sites were situated in the reserve's buffer zone, the proportion of forest specialists was large, but we missed several more secretive and scarcer forest undergrowth species, such as Grey Ground Thrush *Zoothera princei*. Its occurrence is probably restricted to the core zone of the reserve. Given the heavy hunting pressure, Congo Peacock *Afropavo congensis* could be extirpated in Y-MAB (Toirambe *et al.* 2010). Because smaller birds are reportedly scarcely impacted by hunting (Sekercioğlu 2012), their functional shifts are mainly caused by land-use changes or deforestation. This is the case for the forest specialists, absent from degraded habitat (*cf.* Dranzoa 1998), especially insectivores.

Omnivores increase with forest modification (Owiunji & Plumptre 1998, Dale *et al.* 1999). They were rather common, especially Yellow-whiskered Greenbul. However, some studies have reported that omnivorous bird species richness does not differ between habitats (Waltert *et al.* 2005).

Just one other study known to us (Fjeldså 1999) has replicated our discovery of a slight reduction in numbers of small birds with mixed nectar/insect diet in disturbed zones. This contradicts other Afrotropical studies, in which nectarivores are more numerous in degraded forest (Plumptre 1997, Owiunji & Plumptre 1998, Dale *et al.* 1999, Owiunji 2001, Waltert *et al.* 2005, Newmark 2006), presumably because there are greater numbers of flowers in more open habitats. Our dataset may be too limited to detect significant shifts among the smaller feeding guilds.

The only capture of an obligate frugivore was in the transition zone. Other studies in Africa have also discovered that frugivorous birds are more numerous in disturbed areas (e.g. Plumptre 1997, Owiunji & Plumptre 1998, Fjeldså 1999, Owiunji 2001, Naidoo 2004), probably because of the greater abundance of fruiting plants. Elsewhere, frugivorous species richness did not differ between habitats (Waltert *et al.* 2005). Lehouck *et al.* (2009) found some frugivores to be more abundant in more mature forest sites.

The presence of more granivores in the open-habitat matrix reflects their foraging habits, and is similar to the findings of other tropical studies (Sekercioğlu *et al.* 2002, Waltert *et al.* 2005), especially due to the increased presence of grasses in open agricultural areas.

Overall, we can confirm that guild patterns in the central Congo Basin are largely similar to those elsewhere (Plumptre 1997, Waltert *et al.* 2005).

Conclusions

In our survey of the understorey avifauna in Y-MAB, certain forest-dependence classes showed pronounced differences in presence between habitats, as did certain feeding guilds. The similar relative abundances in both forest habitats (old-growth forest and regrowth forest) are due to the 'substitution' of functional groups, with forest specialists being replaced by generalists and insectivores by omnivores, as forest becomes more degraded. These changes result in less specialised bird communities with altered proportions among functional groups. Such shifts may affect ecosystem services despite the high species richness in disturbed forests. Our findings indicate that forest habitat deterioration threatens insectivores, as revealed by most other tropical studies. Doubtless, further land use (particularly agriculture) in the buffer zone of Y-MAB will diminish the forest surface. We suggest that the retention of a mosaic of old-growth forest patches should be considered, as a method of conservation management. It could help maintain resident forest bird populations and their related ecosystem services, particularly invertebrate pest control by insectivores.

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References

Bapeamoni, A. 2014. Biodiversité et densité des nids des oiseaux dans un dispositif permanent à Yoko (RDC). Thèse de doctorat. Kisangani: Université de Kisangani.

Bennun, L., Dranzoa, C. & Pomeroy, D. 1996. The forest birds of Kenya and Uganda. *J. East Afr. Nat. Hist.* 85: 23–48.

Brosset, A. 1982. The social life of the African forest Yellow-whiskered Greenbul *Andropadus latirostris*. *Z. Tierpsychol.* 60: 239–255.

Brosset, A. 1990. A long term study of the rain forest birds in M'Passa (Gabon). In Keast, A. (ed.) *Biogeography and Ecology of Forest Bird Communities*. The Hague: SPB Academic Publishing.

Brown, L. H., Urban, E. K. & Newman, K. 1982. *The Birds of Africa*. Vol. 1. London, UK: Academic Press.

Catry, P., Araujo, A., Cruz, C., Pinheiro, A., Pocas, M., Nadum, J., Armelin, M. & Pereira, J. R. 1999. Are mist-nets suitable for rapid habitat evaluations in the tropics? Results from a study in Guinea-Bissau. *Ostrich* 70: 134–137.

Chapin, J. P. 1932. The birds of the Belgian Congo. Part I. *Bull. Amer. Mus. Nat. Hist.* 65: 1–756.

Dale, S., Mork, K., Solvang, R. & Plumptre, A. 1999. Edge effects on the understory bird community in a logged forest in Uganda. *Conserv. Biol.* 14: 265–276.

Demey, R. & Louette, M. 2001. Democratic Republic of Congo. In Fishpool, L. D. C. & Evans, M. I. (eds.) *Important Bird Areas in Africa and Associated Islands: Priority Sites for Conservation*. Newbury: Pisces Publications & Cambridge, UK: BirdLife International.

Dowsett, R. J., Atkinson, P. W. & Caddick, J. A. 2015. Checklist of the birds of Democratic Republic of Congo. www.africanbirdclub.org (accessed October 2014).

Dranzoa, C. 1998. The avifauna 23 years after logging in Kibale National Park, Uganda. *Biodiver. Conserv.* 7: 777–797.

Dranzoa, C. 2001. Breeding birds in the tropical rain forests of Kibale National Park, Uganda. *Afr. J. Ecol.* 39: 74–82.

Dunham, A. E. 2008. Above and below ground impacts of terrestrial mammals and birds in a tropical forest. *Oikos* 117: 571–579.

Farwig, N., Sajita, N. & Böhning-Gaese, K. 2009. Corrigendum to 'Conservation value of forest plantations for bird communities in western Kenya'. *Forest Ecol. Manag.* 258: 1731–1734.

Fjeldså, J. 1999. The impact of human forest disturbance on the endemic avifauna of the Udzungwa Mountains, Tanzania. *Bird Conserv. Intern.* 9: 47–62.

Fry, C. H. & Keith, S. (eds.) 2004. *The Birds of Africa*. Vol. 7. London, UK: Christopher Helm.

Fry, C. H., Keith, S. & Urban, E. K. (eds.) 1988. *The Birds of Africa*. Vol. 3. London, UK: Academic Press.

Fry, C. H., Keith, S. & Urban, E. K. (eds.) 2000. *The Birds of Africa*. Vol. 6. London, UK: Academic Press.

de Haulleville, T., Kearsley, E., Kidimbu, A., Toirambe, B. & Beeckman, H. 2013. COBIMFO permanent sampling plots in the Yangambi Reserve. Internal rep. (version 20/02/13).

Keith, S., Urban, E. K. & Fry, C. H. (eds.) 1992. *The Birds of Africa*. Vol. 4. London, UK: Academic Press.

Lehouck, V., Spanhove, T., Colson, L., Adringa-Davis, A., Cordeiro, N. J. & Lens, L. 2009. Habitat disturbance reduces seed dispersal of a forest interior tree in a fragmented African cloud forest. *Oikos* 118: 1023–1034.

Louette, M., Bijnens, L., Upoki Agenong'a, D. & Fotso, R. C. 1995. The utility of birds as bioindicators: case studies in equatorial Africa. *Belg. J. Zool.* 125: 157–165.

Ngabo, C. K. M. & Dranzoa, C. 2001. Bird communities in gaps of Budongo Forest Reserve, Uganda. *Ostrich* Suppl. 15: 38–43.

Naidoo, R. 2004. Species richness and community composition of songbirds in a tropical forest-agricultural landscape. *Anim. Conserv.* 7: 93–105.

Newmark, W. D. 2006. A 16-year study of forest disturbance and understory bird community structure and composition in Tanzania. *Conserv. Biol.* 20: 122–134.

Owiunji, I. 2001. Bird recovery in a recently logged forest of Budongo. *Ostrich* Suppl. 15: 56–59.

Owiunji, I. & Plumptre, A. J. 1998. Bird communities in logged and unlogged compartments in Budongo Forest, Uganda. *Forest Ecol. Manag.* 108: 115–126.

Plumptre, A. J. 1997. Shifting cultivation along the Trans-African Highway and its impact on the understorey bird community in the Ituri Forest, Zaire. *Bird Conserv. Intern.* 7: 317–329.

Schouteden, H. 1948–60. De Vogels van Belgisch Congo en van Ruanda-Urundi. *Ann. Mus. Cong. Belge, Zool., sér.* 4: 2(1–3), 3(1–2), 4(1–2), 5(1–3).

Sekercioğlu, C. H. 2002. Effects of forestry practices on vegetation structure and bird community of Kibale National Park, Uganda. *Biol. Conserv.* 107: 229–240.

Sekercioğlu, C. H. 2012. Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. *J. Ornithol.* 153: S153–S161.

Sekercioğlu, C. H., Ehrlich, P. R., Daily, G. C., Aygen, D., Goehring, D. & Sandi, R. 2002. Disappearance of insectivorous birds from tropical forest fragments. *Proc. Natl. Acad. Sci. USA* 99: 263–267.

Sinclair, I. & Ryan, P. 2010. *Birds of Africa South of the Sahara*. Second edn. Cape Town: Struik.

Toirambe, B., Mukinzi, J. C., Onotamba, P., Solia, S. & Nsenga, L. 2010. *Projet d'appui au développement d'un modèle participatif pour l'exploitation durable des ressources naturelles par les populations des zones forestières périphériques dans les forêts tropicales humides du Bassin du Congo - Rapport de l'évaluation de départ de la situation de la Réserve de Biosphère de Yangambi*. Kinshasa: WWF-RDC.

Upoki, A. 2001. Etude du peuplement en Bulbuls (Pycnonotidae, Passeriformes) dans la Réserve forestière de Masako à Kisangani (R.D. Congo). Thèse de doctorat. Kisangani: Université de Kisangani.

Urban, E. K., Fry, C. H. & Keith, S. (eds.) 1986. *The Birds of Africa*. Vol. 2. London, UK: Academic Press.

Urban, E. K., Fry, C. H. & Keith, S. (eds.) 1997. *The Birds of Africa*. Vol. 5. London, UK: Academic Press.

Voelker, G., Marks, B. D., Kahindo, C., A'genonga, U., Bapeamoni, F., Duffie, L. E., Huntley, J. W., Mulotwa, E., Rosenbaum, S. A. & Light, J. E. 2013. River barriers and cryptic biodiversity in an evolutionary museum. *Ecol. Evol.* 3: 536–545.

Waltert, M., Bobo, K. S., Sainge, N. M., Fermon, H. & Muhlenberg, M. 2005. From forest to farmland: habitat effects on Afrotropical forest bird diversity. *Ecol. Appl.* 15: 1351–1366.

Woog, F., Renner, S. C. & Fjeldså, J. 2010. Tips for bird surveys and censuses in countries without existing monitoring schemes. *ABC Taxa* 8: 558–586.

WWF. 2012. Ecoregions of the Democratic Republic of the Congo. *The Encyclopedia of Earth*. www.eoearth.org/view/article/179962 (accessed 31 July 2013).

[a] *Ornithology Section, Biology Department, Royal Museum for Central Africa, Leuvensesteenweg 13, B-3080 Tervuren, Belgium. E-mail: stijn.cooleman@gmail.com*

[b] *Département d'Écologie et de Gestion des Ressources Animales, Faculté des Sciences, Université de Kisangani (UNIKIS), BP 2012, Kisangani, République Démocratique du Congo, E-mail: bapeamonifrank@gmail.com*

[c] *Terrestrial Ecology Unit, Department of Biology, Ghent University, K. L. Ledeganckstraat 35, B-9000 Ghent, Belgium.*

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Appendix 1. Bird species recorded in the Yangambi Man and Biosphere Reserve, DR Congo, 5–24 September 2012.

Sequence and taxonomy follow Dowsett *et al.* (2014).

Biome: GCF = Restricted to the Guinea-Congo Forests biome (Fishpool & Evans 2001).

Forest-dependence (Bennun *et al.* 1996; *BoA*): FF = forest specialist, F = forest generalist, o = forest visitor or open-habitat species.

Feeding guilds (Waltert *et al.* 2005; *BoA*): F = Frugivore, G = Granivore, N = Nectarivore, O = Omnivore, I = Insectivore, C = Carnivore.

Numbers indicate capture rate (birds/100 mnh; 1 mnh = 1 metre-net-hour).

Annexe 1. Espèces d'oiseaux recensés dans la Réserve de biosphère de Yangambi, RD Congo, 5–24 septembre 2012.

L'ordre et la taxonomie suivent Dowsett *et al.* (2014).

Biome : GCF = Espèces confinées au biome de la forêt guinéo-congolaise (Fishpool & Evans (2001).

Dépendance de la forêt (Bennun *et al.* 1996 ; *BoA*) : FF = spécialiste forestier, F = généraliste forestier, o = visiteur forestier ou espèce d'habitat ouvert.

Guildes alimentaires (Waltert *et al.* 2005 ; *BoA*) : F = Frugivore, G = Granivore, N = Nectarivore, O = Omnivore, I = Insectivore, C = Carnivore.

Les nombres indiquent le taux de capture (oiseaux/100 mnh ; 1 mnh = 1 mètre-filet-heure).

		Biome	Forest dependence	Feeding guild	Transition zone	Regrowth forest	Old growth forest	Overall
ACCIPITRIDAE								
Red-chested Goshawk	*Accipiter toussenelii*		FF	C			0.004	0.003
Chestnut-flanked Sparrowhawk	*Accipiter castanilius*	GCF	FF	C		0.011		0.003
COLUMBIDAE								
Blue-headed Wood Dove	*Turtur brehmeri*	GCF	FF	G	0.017			0.003
Tambourine Dove	*Turtur tympanistria*		F	G		0.021		0.005
Blue-spotted Wood Dove	*Turtur afer*		o	G		0.011		0.003
CUCULIDAE								
Olive Long-tailed Cuckoo	*Cercococcyx olivinus*	GCF	FF	I		0.011		0.003
African Emerald Cuckoo	*Chrysococcyx cupreus*		F	I			0.004	0.003
ALCEDINIDAE								
African Dwarf Kingfisher	*Ceyx lecontei*	GCF	FF	I			0.017	0.010
African Pygmy Kingfisher	*Ceyx pictus*		o	I			0.004	0.003
CAPITONIDAE								
Speckled Tinkerbird	*Pogoniulus scolopaceus*	GCF	F	O	0.017	0.032		0.010
Yellow-rumped Tinkerbird	*Pogoniulus bilineatus*		F	F	0.017			0.003
PICIDAE								
African Piculet	*Sasia africana*	GCF	FF	I			0.004	0.003
Buff-spotted Woodpecker	*Campethera nivosa*	GCF	F	I		0.021	0.022	0.018
EURYLAIMIDAE								
Rufous-sided Broadbill	*Smithornis rufolateralis*	GCF	FF	I			0.009	0.005
PYCNONOTIDAE								
Little Greenbul	*Andropadus virens*		F	O	0.017	0.042	0.009	0.018
Yellow-whiskered Greenbul	*Andropadus latirostris*		F	O	0.628	0.573	0.501	0.538
	Andropadus latirostris / virens		F	O	0.017	0.021	0.017	0.018
Simple Greenbul	*Chlorocichla simplex*	GCF	F	O	0.035			0.005
Icterine Greenbul	*Phyllastrephus icterinus*	GCF	FF	I		0.085	0.263	0.180
Xavier's Greenbul	*Phyllastrephus xavieri*	GCF	FF	I	0.017	0.011	0.112	0.073
	Phyllastrephus icterinus / xavieri		FF	I			0.022	0.013
White-throated Greenbul	*Phyllastrephus albigularis*	GCF	FF	I		0.042		0.010
	Phyllastrephus sp. / *Illadopsis* sp.		FF	I	0.035	0.085	0.017	0.037
Red-tailed Bristlebill	*Bleda syndactylus*	GCF	FF	I			0.060	0.037
Red-tailed Greenbul	*Criniger calurus*	GCF	FF	I		0.011	0.009	0.008
Western Nicator	*Nicator chloris*	GCF	F	I		0.021		0.005
TURDIDAE								
Forest Robin	*Stiphrornis erythrothorax*	GCF	FF	I			0.004	0.003
Fire-crested Alethe	*Alethe diademata*	GCF	FF	I			0.035	0.021
Rufous Flycatcher Thrush	*Stizorhina fraseri*	GCF	FF	I		0.021	0.022	0.018
SYLVIIDAE								
Yellow Longbill	*Macrosphenus flavicans*	GCF	FF	I		0.011	0.004	0.005

		Biome	Forest dependence	Feeding guild	Transition zone	Regrowth forest	Old growth forest	Overall
Green Hylia	*Hylia prasina*	GCF	F	I	0.070	0.117	0.048	0.068
CISTICOLIDAE								
Tawny-flanked Prinia	*Prinia subflava*		*o*	I		0.011		0.003
Green-backed Camaroptera	*Camaroptera brachyura*		*o*	I	0.035	0.021	0.004	0.013
Yellow-browed Camaroptera	*Camaroptera superciliaris*	GCF	FF	I	0.017			0.003
MUSCICAPIDAE								
Fraser's Forest Flycatcher	*Fraseria ocreata*	GCF	F	I		0.011		0.003
Yellow-footed Flycatcher	*Muscicapa sethsmithi*	GCF	FF	I			0.009	0.005
Grey-throated Tit-Flycatcher	*Myioparus griseigularis*	GCF	FF	I	0.017			0.003
MONARCHIDAE								
(African?) Paradise Flycatcher	*Terpsiphone* (*viridis*)		*o*	I		0.021	0.022	0.018
Red-bellied Paradise Flycatcher	*Terpsiphone rufiventer*	GCF	FF	I		0.011	0.022	0.016
PLATYSTEIRIDAE								
Chestnut Wattle-eye	*Dyaphorophyia castanea*	GCF	FF	I		0.042	0.030	0.029
TIMALIIDAE								
Pale-breasted Illadopsis	*Illadopsis rufipennis*		FF	I	0.017	0.011	0.004	0.008
Brown Illadopsis	*Illadopsis fulvescens*	GCF	FF	I	0.017	0.011		0.005
Scaly-breasted Illadopsis	*Illadopsis albipectus*	GCF	FF	I			0.013	0.008
	Illadopsis sp.		FF	I		0.011		0.003
NECTARINIIDAE								
Grey-headed Sunbird	*Deleornis axillaris*	GCF	FF	I			0.013	0.008
Blue-throated Brown Sunbird	*Cyanomitra cyanolaema*	GCF	FF	N		0.011	0.004	0.005
(Western Olive?) Sunbird	*Cyanomitra* (*obscura*)		FF	N	0.122	0.127	0.242	0.196
Collared Sunbird	*Hedydipna collaris*		F	N			0.004	0.003
Olive-bellied Sunbird	*Cinnyris chloropygius*		F	N		0.032		0.008
PLOCEIDAE								
Vieillot's Black Weaver	*Ploceus nigerrimus*	GCF	o	O	0.035			0.005
ESTRILDIDAE								
Chestnut-breasted Negrofinch	*Nigrita bicolor*	GCF	FF	I		0.011		0.003
Jameson's Antpecker	*Parmoptila jamesoni*	GCF	FF	I			0.004	0.003
Orange-cheeked Waxbill	*Estrilda melpoda*		*o*	G	0.017			0.003
Grant's Bluebill	*Spermophaga poliogenys*	GCF	FF	G			0.022	0.013
Western Bluebill	*Spermophaga haematina*	GCF	F	G	0.052		0.009	0.013
Total capture rates (birds/100 mnh) in metre-net-hour					1,205	1,475	1,589	1,504
Total number birds captured					69	139	368	576
Shannon-Wiener index					1.96	2.50	2.47	
Total numbers of species captured		35			17	28	32	51
Capture rate (birds/100 mnh)	FF				0.262	0.520	0.946	0.739
	F				0.855	0.891	0.613	0.718
	o				0.087	0.064	0.030	0.047